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Hen Harrier *Circus cyaneus* nest sites on the Isle of Mull are associated with habitat mosaics and constrained by topography

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Summary

Capsule: Hen Harrier on the Isle of Mull, UK, are associated with habitat mosaics consisting of moorland, scrub and forestry but avoid grazed land, suggesting that forested habitats could be managed sympathetically for Hen Harrier in the future should the current UK population increase.

Aims: To use distribution modelling to investigate nesting habitat associations using a long term dataset for Hen Harrier on Mull.

Methods: We develop area-interaction models using a LASSO penalty to explore the distribution of 102 Hen Harrier nest sites in relation to habitat and topography. Our model is then successfully validated in tests using data for 70 nest sites from subsequent years.

Results: Our model is effective in predicting suitable areas for Hen Harrier nest sites and indicates that Hen Harriers on Mull are found in habitat mosaics below 200 m asl. Hen Harrier nest intensity is positively associated with increasing proportions of moorland and scrub, open canopy forestry and closed canopy forestry. Nest intensity is negatively associated with increasing proportions of grazed land.

Conclusion: Hen Harrier avoid grazed areas but are relatively tolerant of other habitat combinations. These findings are supported by previous observations of Hen Harrier habitat use and have implications for the recovery of some Hen Harrier SPA populations and future forest management. Open canopy forest and forest mosaics could potentially be incorporated into landscape-scale conservation plans for Hen Harriers using the population in Mull as an example.

1. Introduction

In anthropogenic landscapes such as upland Britain, management and protection of species of conservation concern present a complex challenge (Geary et al., 2015). Understanding species distributions both at the scale of species ranges and in terms of their distribution across available habitats is an integral part of species conservation and ecosystem management (Elith and Leathwick, 2009). Methods for the modelling and prediction of species' distributions cover a wide range of statistical and methodological techniques (Elith and Graham, 2009). Many share the common assumption that the species' distribution is in equilibrium within the landscape (Araújo and Pearson, 2005). This assumption has been relaxed in certain situations in particular when predicting the spread of invasive species (Gallien et al., 2012) or species responses to novel environmental conditions (Berry et al., 2002). However, as models of invasive range expansion demonstrate, the results can differ depending on whether data are sourced from the native range (presumably close to equilibrium) or the invasive range (potentially not in equilibrium; Loo et al., 2007).

Modelling species distributions, and investigating drivers delimiting those distributions, when the data available contain only presences provides some methodological difficulty (Hastie and Fithian, 2013). Breeding raptor surveys often result in presence only data as survey methods are targeted towards identifying occupied nest sites within the landscape and, as such, absences are implied by lack of presence rather than specifically recorded (Hardey, 2006). Until recently the machine learning method MaxEnt proved to be successful in modelling distributions using presence only data (Phillips and Dudík, 2008) but was the subject of some scrutiny due to its 'black box' nature (Royle et al., 2012) and because default parameters were often used unquestioningly resulting in loss of accuracy in models (Warren and Seifert, 2011). Recently a mathematical equivalence between MaxEnt and regression models using a LASSO penalty (Renner and Warton, 2013) has been demonstrated. Point process models which use a background sample of quadrature points to delimit the environmental space of the species distribution can be used with LASSO penalties to model species distributions using presence-only data (Renner et al., 2015). The LASSO penalty reduces overfitting by constraining parameter estimates – called ‘regularisation’ in MaxEnt (Warton et al., 2013). Point process models predict the relative intensity, in terms of presence records per unit area, across the region of interest (Renner et al., 2015). A statistical explanation of how point process models are used to model species distributions can be found in Renner (2013).

Hen Harrier *Circus cyaneus* is a medium sized, ground nesting raptor which, along with the closely related Northern Harrier *Circus hudsonius,* has a circumpolar boreal distribution (Sangster et al., 2016). Although Hen Harrier is considered to be of least concern globally (BirdLife International, 2015) it is of conservation importance in Great Britain and Ireland (Fielding et al., 2011). Hen Harrier are thought to have adapted to foraging in open landscapes over a long period of time (Simmons, 2000). They are known to forage extensively on field voles *Microtus agrestis*, young lagomorphs and small moorland passerines (Redpath et al., 2001; Smith et al., 2001). In mainland Britain the distribution of Hen Harrier is thought to be limited not solely by environmental conditions but by anthropogenic intervention (Anderson et al., 2009). The current status and distribution of Hen Harrier in Britain is thought to be strongly influenced by persecution, especially on moorland managed for sporting interests, in particular the driven shooting of red grouse *Lagopus lagopus* (Etheridge et al., 1997; Fielding et al., 2011). The recent population estimate of approx 660 breeding pairs is located mainly in Scotland with major strongholds on Orkney, the Hebrides, Arran, mainland Argyll, Ayrshire and Dumfries and Galloway (Hayhow et al., 2013). The UK Hen Harrier population was surveyed in 2016 and the results from this survey will indicate if those strongholds are still extant although anecdotal evidence suggests that the Ayrshire and Dumfries and Galloway population has collapsed (Haworth pers comm.). With a more enlightened attitude on grouse moors the UK population could expand to perhaps 2500 pairs (Fielding et al., 2011). The presence of large Hen Harrier populations on the Isle of Man (Hayhow et al., 2013; Sim et al., 2007) and outside the UK suggests that a wider range of nesting habitats than heather moor might prove suitable for Hen Harrier.

Previous work on the distribution of Hen Harrier found a range of factors to be important in delimiting their distribution including topography, environmental drivers and species interactions. Tapia et al., (2004) used logistic regression to predict the presence/absence of Hen Harrier and Montagu's Harrier *Circus pygargus* in NW Spain where Hen Harrier presence was associated with fewer human settlements and the slope was less steep in occupied habitat. However, the final model was relatively uninformative in that it only retained minimum elevation as a predictor. Tapia et al., (2004) suggested that the main threats for Hen Harrier in their study region came from the proliferation of roads and massive afforestation of open scrub-pasture land. Cormier et al., (2008) also modelled the nesting habitat of Hen Harrier and Montagu's Harrier, but this time in central France (Poitou-Charentes region). They used two methods, discriminant function analysis and regression trees and concluded that the factors determining Hen Harrier nest selection were unclear but nests were usually found in plots where bosom heath *Erica scoparia* was > 1.87 m tall and that afforestation did not seem to benefit Hen Harrier. Massey et al., (2009) used a classification tree approach to model the distribution of the similar Northern Harrier on Nantucket Island (Cape Cod, Massachusetts). Their approach compared habitat, as measured by 70 landscape metrics, within 50 m, 200 m, 500 m and 1,000 m of nests sites and random locations. Classification trees were used to identify two important nesting habitats. The first was in, or adjacent to, wetlands and the second was in drier upland habitats. Both of these, as in the Tapia et al., (2004) study, shared an avoidance of developed land and forests, although this was less marked in wetlands.

Anderson et al., (2009) used generalised linear models at two resolutions to model Hen Harrier distributions in the UK. They found no support for their hypothesis that climate directly determines the current UK distribution and although their habitat model was more successful it failed to predict some of the more important Scottish populations (e.g. Islay, Arran and the Uists). However, some of the problems with their model are probably related to the restricted Hen Harrier distribution data available to them. The status on Hen Harrier on the British mainland may also influence investigations on their distribution as they are absent from many areas in which suitable habitat is present and there is historical evidence of occupation (Hayhow et al., 2013).

On the Isle of Mull, one of the Inner Hebrides, where a small population of breeding harriers was established in the north and east by the late 1960s and early 1970s (Sharrock, 1976), grouse moor and the anthropogenic pressures associated with this habitat are absent so the species may be occupying a more natural range of habitats. Results for the recent (2016) national survey suggest that this population now represents around 8% of the Scottish Hen Harrier population (Haworth pers. comm.). However, it should also be noted that Mull, much like the majority of the Scottish highlands, is far from a natural landscape with economically driven land use such as agriculture and commercial forestry predominating (Warren, 2002). The shorter vegetation of most land used for agriculture results in less prey and suitable Hen Harrier nesting habitats. However, there is strong evidence that afforestation is beneficial in the early pre-thicket stages, providing good cover for nests and an abundance of voles (Madders, 2000; Redpath et al., 1998). Subsequent canopy closure reverses this, although in some forests large patches of failed trees or unplanted ground develop into rank dwarf shrub and harriers continue to breed in such areas suggesting that there may be opportunities for forest planting schemes that are beneficial for Hen Harrier.

Land use change will continue to affect grazing regimes and woodland management and economic pressures might result in wide scale changes in land use as they have in the past

(Warren, 2002). Recently, the Irish National Parks and Wildlife Service completed a comprehensive review of the literature related to Hen Harrier ecology and forests (NPWS, 2015) and the 2015 National Survey of Breeding Hen Harrier in Ireland (Ruddock et al., 2016) found that Hen Harrier in Ireland were most frequently recorded to forage in open non-afforested habitats (51.3%) compared to afforested habitats (40.6%) but recorded more frequently to nest in second rotation forest (58.3%) than heather moorland (25.9%). It is important therefore, to have a better understanding of Hen Harrier habitat requirements and an awareness of undesirable habitat. In particular, it is important in the case of the Hen Harrier to explore habitat preferences in areas where persecution and disturbance are rare so that absences are more likely to reflect habitat drivers rather than human interference. The distribution and habitat use of Hen Harrier on the Hebrides can help to shed light on this area of research. Here we use records of Hen Harrier nesting locations and habitat data on the Isle of Mull to investigate drivers of Hen Harrier distribution using a point-process regression model (Renner et al., 2015). This model will aid habitat and landscape managers to develop conservation strategies for Hen Harrier under scenarios where anthropogenic pressures are reduced and also provide a framework for modelling other Hen Harrier populations and other species.

2. Methods

2.1 Study area

Mull (56° 27’N 06° 00’W) covers 875 km^2 (924 km^2 including all subsidiary islands) and is the third largest of the Hebridean islands. Although Mull has a characteristic terraced landscape, derived from the predominant basaltic lava flows, there are also significant regions of schist, granite and sedimentary rock. The centre of the island is dominated by Ben More (966 m) and its surrounding mountains. Much of Mull is used for sheep and cattle grazing, although sheep densities are lower than many areas in the western Highlands and Islands of Scotland (Fuller and Gough, 1999). There are also large numbers of Red Deer *Cervus elaphus* (average density about 10 deer per km^2) and several hundred feral goats *Capra hircus*. Numbers of Red Grouse and Ptarmigan *Lagopus mutus*, common prey of Golden Eagles *Aquila chrysaetos* and some other raptors in many parts of Scotland, are low but there are significant numbers of the introduced Irish Mountain Hare *Lepus timidus hibernicus* and Rabbits *Oryctolagus cuniculus* are common in some coastal locations. Approximately 13,900 ha (or 15% of the island) is covered with commercial conifer plantations (including recently felled plantation), partly on ground owned by Forestry Commission Scotland (FCS) but also by private and community ownership. The current trend is mainly towards schemes for planting or regeneration of native deciduous species under the UK government's Woodland Grant Schemes (WGS), which provides grant aid for establishing and early management of private woodland areas. However, the recent trend on the island has been an increase in felling with the National Forest Inventory indicating that the area of felled forest more than doubled between 2012 and 2014. Felling has been accompanied by an increase in ground preparation which suggests an increase in forest areas over the coming decade (Forest Research, 2013). Recently around 20% of the commercial forestry on Mull has been felled but is likely to be replanted in the future (Forest Research, 2016). In the same time period a similar amount of native woodland has been planted (Forestry Commission, 2014).

2.2 Data

Species data, Hen Harrier breeding locations, were collected in the field by PFH. As is often the case with ecological data from monitoring programmes, only species presence was recorded as nests were actively sought across the island. Surveys for breeding harriers were undertaken from April until August according the methods set out in (Hardey, 2006). Surveys for Hen Harrier nest locations (n = 102) were carried out each year between 2005 and 2014. Surveyed sites were spread across the island, often in conjunction with golden eagle surveys, and were not restricted to particular parts of the island and surveyed areas were not fixed across the years. The number of nests located per year varied between 12 (2006, 2009 and 2013) and 30 (2008), The median was 14 nests per year. In 2015 and 2016 the survey effort was increased to more than 60 days of dedicated Hen Harrier field surveys spread across the entire island. The aim was to provide a large data set that could be used for model validation. Data from 2015 (n=28) and 2016 (n=42) was retained for model testing. Topographic data were derived from the Ordnance Survey 50 m Digital Terrain Model (DTM), version 04/2010 supplied under the Ordnance Survey OpenData Licence. In addition to elevation, slope was calculated using the slope() function of the raster package (Hijmans and van Etten, 2012) in R (R Core Team, 2016). Habitat data were taken from Land Cover Map 2007 (LCM 2007) from the Centre for Ecology and Hydrology (Morton et al., 2011) and National Forest inventory 2013 (downloaded from the Forestry Commission Scotland; Forest Research 2013). LCM categories which represented grazed land (LCM2007 classes 3 – 8) and moorland or scrub (LCM2007 classes 9 – 12) as well as National Forest Inventory categories which represented open canopy forest (young forest and shrub) and closed canopy forest (coniferous, broadleaved and mixed) were selected for use in modelling. The proportion of each habitat type within a 1.1 km square surrounding each pixel was calculated using the focal () function of the ‘raster’ package in R (Hijmans and van Etten, 2012) . Both the DTM and slope data were resampled in order to match the cell size and extent with the classified habitat raster files.

2.3 Species distribution model

Here we use a point process model with a LASSO penalty to model the intensity of Hen Harrier nest sites across Mull using elevation, slope, proportion of grassland/moorland, proportion of moorland and scrub, and proportion of both open canopy and closed canopy forest. All models were fitted using the ppmlasso package (Renner and Warton, 2013) in R. The design matrix for the model consisted of the variables themselves along with quadratic terms for the proportion of grazed land and elevation because Hen Harriers have been previously shown to prefer intermediate values for each of these variables (Fielding et al., 2011). Using quadratic terms for the two forest categories did not alter the predicted relationship so simpler terms were preferred. The optimal LASSO penalty was selected from 1000 model fits by minimising the Bayesian information criterion (BIC; Renner et al., 2015). The resolution for quadrature points used in the models was found using the findres() function in ppmlasso which showed that a resolution of 100m (compared to 1000, 500, 400, 300, 200, 150, 120 and 110 m) gave the highest likelihood value without violating the assumptions of the model. The initial fitted model showed significant clustering at distances below 1000 m when compared to simulated Ripley’s K envelopes (Baddeley and Turner, 2005) so an area-interaction model was preferred with a radius of point interaction of 200 m. This interaction is likely to be caused by pairs using similar nesting sites across the years surveyed but also because of locations where different nests are close to each other. The area-interaction model reduces the impact of these similar nesting sites on the overall point process. Although the profilepl() function in the ‘spatstat’ package (Baddeley and Turner, 2005) suggested a radius of 800m as optimal, a radius of 200m reduced spatial bias in the residuals. Radii between 50 and 2500 m were considered as potential point interaction settings based on Ripley’s K plots for the point process models. The value for the radius of point interactions was chosen by comparing the fit of models with different *r* values to simulated realisations of a fitted Gibb’s model (Renner et al., 2015). Model residuals were evaluated both spatially and using lurking variable plots. Predicted intensities were calculated by projecting the fitted model onto data for the whole island and converted to intensities per 1 km^2.

2.4 Model validation

Models were validated using Hen Harrier nest locations collected in 2015 and 2016 (n = 70) as test data with which to compare model predictions. To validate the models we used both the area under the curve (AUC) of the receiver operating characteristic (ROC) plot (Fielding and Bell, 1997) as well as the True Skill Statistic (TSS; Allouche et al., 2006). AUC ranges between 0 and 1 with scores over 0.75 considered to represent good predictive power (Pearce and Ferrier, 2000). TSS ranges between -1 and 1 with values closer to 1 representing higher predictive accuracy (Allouche et al., 2006). The predicted intensity map from the area interaction model was rescaled (range 0 and 1) as a proportion of the maximum prediction. A threshold between presence and absence is required and we chose the maximum sum of sensitivity and specificity (Liu et al., 2005). Both were calculated using 100 background points in place of the unavailable absence values. This calculation was repeated over 1000 iterations using randomly selected background points.

3. Results

The optimum fitted area-interaction model used a LASSO penalty of 0.00005 selected by minimising BIC and predicted highest Hen Harrier nest presence intensity across small areas of Mull (Fig. 1). Although, the predicted nest presence intensity was low in all areas, with a maximum of 0.043 per 1 km^2, low densities are consistent with recorded nesting densities (Fielding et al, 2011). The model (Table 1) showed a positive relationship with the proportion of scrub moorland, proportion of open canopy forestry and proportion of closed canopy forestry. (Fig. 2a) and a positive relationship with forest cover (Fig. 2.b). Hen Harrier nest presence intensity had a negative relationship with increasing proportions of grazed land (Fig. 2d) and increasing elevation (Fig.2e) with evidence of non-linearity shown by the quadratic terms for both variables and a negative relationship with slope (Fig 2f). The area interaction term for the model was positive meaning that there is a tendency within the data for nests to be clustered to some degree. All other terms in the models were reduced to $\beta = 0$ due to the LASSO penalty.

Table 1. Parameter estimates and standard error for the optimum area interaction model using a LASSO penalty of 0.00005, selected by minimising BIC, to predict the intensity of

Hen Harrier nest presence using the proportion of important habitat types on the Isle of Mull, Scotland.

Model term	β	S.E.
Intercept	-19.35	0.05
Proportion of grazed land	-0.37	0.008
Proportion of grazed land^2	-0.23	0.005
Proportion of scrub/moorland	0.28	0.004
Proportion of Open Forest	0.14	0.001
Proportion of closed forest	0.23	0.003
Elevation	-4.3	0.09
Elevation^2	-3.67	0.08
Slope	-0.23	0.005
Area-Interaction term	0.44	0.001

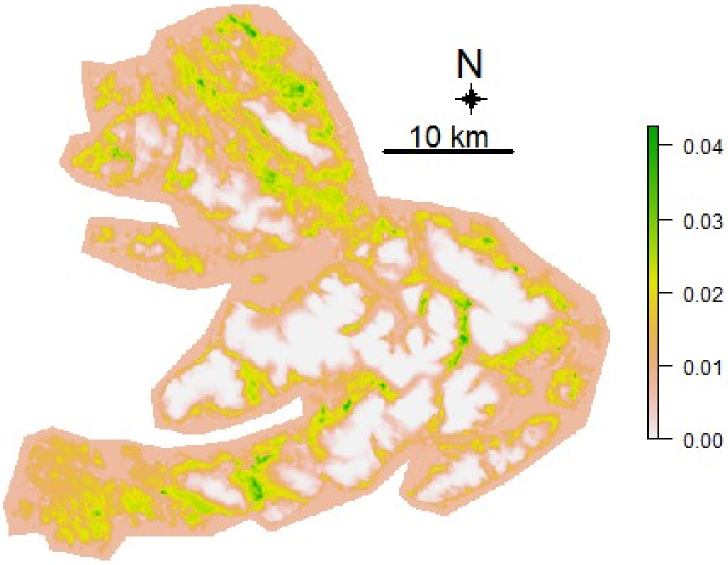

Figure 1. Predicted intensity of Hen Harrier nest presence per 1 km^2 for the optimum area interaction model using a LASSO penalty of 0.00005, selected by minimising BIC, to predict the intensity of Hen Harrier nest presence using the proportion of important habitat types on the Isle of Mull, Scotland.

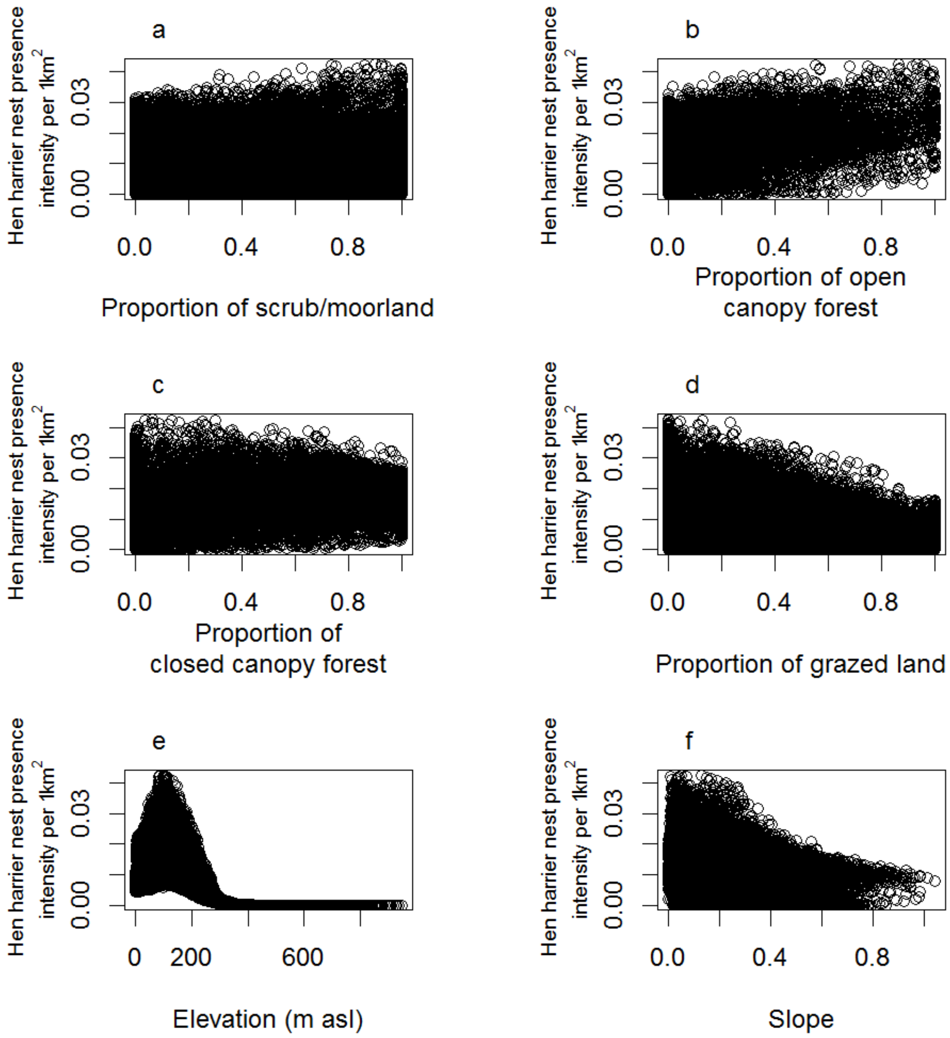

Figure 2. Plots of predicted Hen Harrier nest presence intensity against (a) proportion of scrub/moorland, (b) proportion of open canopy forestry, (c) proportion of closed canopy forestry, (d) proportion of grazed land, (e) elevation and (f) slope for the optimum area interaction model using a LASSO penalty of 0.00005, selected by minimising BIC, to predict the intensity of Hen Harrier nest presence using the proportion of important habitat types on the Isle of Mull, Scotland.

3.1 Model validation

The area-interaction model performed well in terms of predicting suitable areas for nest sites when tested against independent survey data from 2015 and 2016. The median AUC value was 0.82 (range 0.73 – 0.89) and the median TSS was 0.55 (range 0.43 – 0.71). The intensity of Hen Harrier nest locations on Mull was spatially similar to those predicted by the model. In particular, high intensity areas are present in the East and South West of the island which are also present in our predictions. Density in the North of the Island was generally lower and more localised.

4. Discussion

Our area-interaction model indicates that Hen Harrier distribution on Mull is characterised by habitat mosaics of moorland and forest and low proportions of grazed land. The model had good predictive accuracy when tested with data from 2015 and 2016 which demonstrates an ability to predict suitable breeding habitat for Hen Harriers on Mull. The spatial distribution of predicted Hen Harrier intensity reflect the distribution of nests found on the island, however, our predicted intensity was lower than actual intensities which suggests that our models are conservative in their estimates. It is worth noting that extensive island wide surveys for breeding Golden Eagle, White-tailed Eagle *Haliaeetus albicilla* and Hen Harrier since 1982 have yet to locate a single Hen Harrier breeding attempt outwith the predicted areas (Haworth, pers. comm.). Both open and closed canopy forestry were positively associated with Hen Harrier nest intensity, however, response plots showed that, as suggested by previous research, the relationship with open canopy forestry was more clearly positive (Redpath et al., 1998). Elevation and slope were important in determining Hen Harrier distribution on the island, our model indicating that Hen Harriers prefer narrow ranges of both variables with an elevation limit at around 200 m and avoidance of steep slopes. The elevation limit for Hen Harrier recorded on the mainland is around 550 m (Gilbert et al., 2011) which is noticeably higher than on Mull despite the presence of extensive higher ground. Previous models of Hen Harrier distribution have also noted the importance variables related to topography (Tapia et al., 2004). The difference in elevation limit between Mull and mainland Scotland may be due to its topography but could also be due to higher densities of Golden Eagle territories which are thought be avoided by Hen Harriers (Fielding et al., 2011). Our model included an area-interaction term which suggests that Hen Harrier nests are found close to each other within the landscape or similar locations are used in different years. We believe that this clustering reflects clustering among Hen Harrier nest sites due to levels of philopatry, and use of nest sites in subsequent years, within the population (Watson and Thirgood, 2001) or possible evidence of conspecific attraction as seen in Montagu’s harriers (Cornulier and Bretagnolle, 2006). Different methods identified different optimal values for the radius of this area-interaction within our models which suggests that the processes driving this clustering may operate at more than one spatial scale.

Our results suggest that Hen Harriers on Mull prefer open mosaics which can include both forestry categories but avoid open, grazed land. All nests located in 2015 and 2016 were situated in areas with no sheep and cattle grazing although varying numbers of red deer were often present. The use of a range of habitat types but avoidance of grazed land shown in the results is in agreement with findings on Hen Harrier habitat preference in both Scotland (Arroyo et al., 2009) and Ireland (Wilson et al., 2009). Our model shows a response to increasing scrub/moorland cover suggesting that areas with proportions over 80% are optimal. On the Scottish mainland it is often assumed that Hen Harriers show a preference for open moorland (Redpath et al., 1998) and in particular are associated with moorland managed for upland grouse shooting (Thompson et al., 2009). However, our results on the Isle of Mull suggest that Hen Harriers are more diverse in their habitat preference, at least in this population. Higher predicted nest intensities are also associated with areas containing open canopy and closed canopy forest. Hen Harriers only appear to actively avoid areas in which the vegetation height is low. The highest predicted intensities were in areas with less than 20% grazed land. Indeed Hen Harriers are known for using edge habitats for hunting which habitat mosaics are likely to provide (Redpath, 1992; Schipper, 1977) and nesting in tall crops in parts of France (Cormier et al., 2008). Our models suggest that the exact makeup of habitat mosaics can be variable but that either moorland, scrub or open canopy forestry should be the dominant habitat types.

Hen Harriers are known to use first rotation forestry plantations as foraging habitat before canopy closure (Redpath et al., 1998) and have been noted to use second rotation restocked plantations in the same way in Ireland (Wilson et al., 2009). Further clarification is required on the likely use of restocked forests for breeding Hen Harriers and the timeframe for its suitability as nesting habitat. Additionally, further research on the makeup and management of forested areas within Hen Harrier territories will be beneficial. However, our model clearly indicates the importance of forested areas as constituents of suitable areas for breeding Hen Harrier on Mull. In areas where grazing is heavy, pre-thicket plantations can provide more foraging potential than open areas (Madders, 2003). As such, we suggest that more complex habitat mosaics surrounding nest sites have the potential to be used as foraging habitat by Hen Harriers. It is likely that that dense, closed canopy plantation forests may be unsuitable for hen harrier. Indeed our models suggest that territory densities are highest in areas where the proportion of closed canopy forest is low. However, the combinations of habitat variables indicated as suitable by our model indicates that more open forested landscapes with a mixture of vegetation cover can form part of hen harrier territories. The potential nature of these forested areas warrants further investigation with particular emphasis on the appropriate scale of habitat mosaics.

Anderson et al. (2009) suggest that the discrepancy between the predictions of their climatically based and habitat based models may be due to the impact of current and historical persecution. This may be the case for areas such as the North of England where Hen Harriers are currently extremely scarce (Potts, 1998) but the available habitats are similar to those found in ‘suitable’ landscapes for Hen Harriers further to the north. According to our models, Hen Harriers might potentially find ‘suitable’ landscapes across large areas of Britain and Ireland where grazing pressure is not too high (Madders, 2003) if current populations were able to increase to close to carrying capacity. Grouse moors themselves, may be attractive to harriers because of high prey densities due to human management (Smith et al., 2001) rather than features of the habitat itself and can impact on Hen Harrier populations due to reduced breeding success and survival (Green and Etheridge, 1999). More complex habitat mosaics in these areas would potentially provide higher densities of alternative prey items such as meadow pipit *Anthus pratensis* (Vanhinsberg and Chamberlain, 2001). This investigation concentrated on habitat variables and Hen Harrier presence, as such, did not consider the success of Hen Harriers in different habitat types. In order to provide more comprehensive recommendations for upland mosaics, demographic information should be incorporated into habitat models.

Due to the economically driven land use change experienced in working landscapes such as the Scottish uplands (Pack, 2010; Warren, 2002), habitat heterogeneity has decreased during the last century (Benton et al., 2003; Maclean, 2010). Our model suggests that increased habitat heterogeneity could be beneficial for Hen Harrier. This would be potentially also benefit other species, such as Short-eared Owl (Wheeler, 2008) and Black Grouse *Tetrao tetrix (Geary et al., 2013)*. Increasing grazing pressure was implicated in the decline of Hen Harrier populations on Orkney (Amar et al., 2011) and our results would suggest that wider grazing reductions could contribute to beneficial mosaics for Hen Harrier. There is already evidence for a reduction of grazing pressure across Scotland (Fuller and Gough, 1999; Scottish Government, 2003). Due to the economic incentives and current Scottish government targets related to upland afforestation (Scottish Executive, 2006; Warren, 2002), we can expect further increases in tree cover in Britain and Ireland. However, with careful consideration of the structure of the resulting landscapes it is possible to find compromises between land management and conservation outcomes (Polasky et al., 2008).

Our model along with populations on Mull, and other islands, may provide some evidence that landscapes currently considered ‘unsuitable’ due to a lack of Hen Harrier warrant management to make them as Hen Harrier friendly as possible. The exact details of ‘Hen

Harrier friendly' management would benefit from further research as Hen Harrier in other locations are likely to be influenced by other factors to those which are important on Mull. Government policy aims to expand the area under some form of woodland in Scotland from 17% in 2007 to 25% by the second half of this century (Forestry Commission 2009; Forestry Commission 2016). This includes creating 10,000ha per year between 2014 and 2020. This presents an opportunity, via sympathetic management, to enhance the availability of habitat for breeding Hen Harrier although it is important to link breeding habitat with suitable foraging habitat.

In this case we suggest that forestry is integrated more fully into landscape mosaics, that areas with high proportions of open canopy forestry are not overlooked as possible Hen Harrier habitat and that grazing pressure is reduced where possible. The current extent and persistence of harriers breeding in restocked forests is largely unknown but could be an important, even if it is a somewhat locally and regionally transient feature of the harrier population in the future. The evidence from Ireland (Ruddock et al., 2016; Wilson et al., 2009) is that second rotation forest can represent a significant nesting resource for Hen Harriers. At a much more local scale open areas within forests such as those where there is deep peat, and areas left unplanted due to a lack of soil, are also important for nesting harriers (Fielding et al., 2011). The proximity, extent and management of open land surrounding forests is also likely to have a bearing on the success of breeding harriers in terms of potential prey availability and potential predation pressures (Arroyo et al., 2009; Wilson et al., 2012).

4.1 Conclusion

The area interaction model with LASSO penalty was successful in modelling Hen Harrier nest intensity in relation to habitat on Mull. In this case the spatial interaction would have meant that the assumptions of similar models, such as MaxEnt, would have been violated whereas the point-process framework gave us the flexibility to deal with this issue. Our results indicate that Hen Harrier have the potential to occupy a diverse range of habitat types where taller vegetation is available including those with forest cover. As such, wider areas of Britain and Ireland may be suitable for Hen Harrier in the future, given a reduction in persecution and expansion of the current population, if sympathetically managed to include variety of habitat types. Sympathetic management, according to our results, would have implications for forest management across large scales and require further research and long-term planning. Our results provide information on Hen Harrier habitat preference, although not necessarily breeding success or productivity, which can inform future survey work aimed at locating breeding Hen Harrier as our models have proved successful in predicting Hen Harrier nest locations in 2015 and 2016. Using this information surveys can be more targeted, which would be more efficient in terms of effort and less costly. Similarly, maintaining, managing and enhancing areas to encourage breeding Hen Harrier can be more clearly focussed if habitats suitable for breeding are geographically restricted in some regions and, using information on habitat preference, their effectiveness can be maximised as part of economically driven changes. Our work explores these preferences on the Isle of Mull but the same principles could be applied to a wider area across Great Britain and Ireland as part of conservation plans.

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Tables

Table 1. Parameter estimates for the optimum area interaction model using a LASSO penalty of 0.00005, selected by minimising BIC, to predict the intensity of Hen Harrier nest presence using the proportion of important habitat types on the Isle of Mull, Scotland. Confidence intervals (95%) are presented across the 1001 model runs.

Model term	**β**	**95% C.I.**
Intercept	-19.35	0.1
Proportion of grazed land	-0.37	0.02
Proportion of grazed land^2	-0.23	0.01
Proportion of scrub/moorland	0.28	0.01
Proportion of Open Forest	0.14	0.002
Proportion of closed forest	0.23	0.01
Elevation	-4.3	0.18
Elevation^2	-3.67	0.16
Slope	-0.23	0.01
Interaction	0.44	0.002

Figure Legends

Figure 1. Predicted intensity of Hen Harrier nest presence per 1 km^2 for the optimum area interaction model using a LASSO penalty of 1.69, selected by minimising BIC, to predict the intensity of Hen Harrier nest presence using the proportion of important habitat types on the Isle of Mull, Scotland.

Figure 2. Plots of predicted Hen Harrier nest presence intensity against (a) proportion of scrub/moorland, (b) proportion of open canopy forestry, (c) proportion of closed canopy forestry, (d) proportion of grazed land, (e) elevation and (f) slope for the optimum area interaction model using a LASSO penalty of 0.00005, selected by minimising BIC, to predict the intensity of Hen Harrier nest presence using the proportion of important habitat types on the Isle of Mull, Scotland.